

Growth Patterns in the Modern Human Skeleton

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ABSTRACT This study investigates cross sectional growth patterns in the human skeleton using a recent skeletal sample of known age and sex. Measurements were selected to reflect different functional regions of the cranium, mandible and post cranial skeleton, and growth is evaluated using a single phase Gompertz curve. Different parts of the skeleton vary in the proportion of adult size attained at birth and in their subsequent rate of attainment of adult size. The paper introduces a method for the objective and quantitative comparison of the growth of different samples, and is used in this instance to analyze sexual differences in the growth of the post cranial skeleton. The development of sexual dimorphism is evaluated in terms of differences in the rate and duration of male and female growth. Adult sexual dimorphism is generally lower in early growing variables than in later-growing variables. There is considerable diversity in the ontogenetic basis of sexual dimorphism in the human skeleton demonstrating that the development of sexual dimorphism within a species should not be regarded as a uniform phenomenon. *Am J Phys Anthropol* 105:57-72, 1998.

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Within the human body, different functional systems grow at different rates and attain adult size at different stages of overall development. Scammon (1930) demonstrated this variability in the growth of the major organs and soft tissues of the body. Neural structures such as the brain and eyes show rapid early growth and approach adult size during childhood. Body weight and the major organs of the body follow the somatic or general growth pattern and reach adult size after puberty. Within the framework of functional cranial analysis, the growth of each part of the skeleton is explained primarily as a response to the requirements of the associated non-skeletal tissues (Moss, 1973). This allows skeletal measurements to be understood in the wider context of the functioning skull. The body can be considered as a series of functional components, each composed of the soft tissues and spaces used to carry out a given function (the functional matrix) and the

skeletal elements which support and protect the functional matrix (the skeletal unit). The interdependence of the skeleton and associated soft tissue structures provides the basis for the present study, which examines the diversity of growth patterns in the modern human skeleton.

This paper describes a cross sectional analysis of the growth of the cranial and post cranial skeleton using measurements from a collection of identified skeletons. It compares the growth patterns of variables measured throughout the skeleton and identifies variation in the developmental schedule of different functional regions. Such differences have potentially important evolutionary and ecological implications and

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may reflect energetic and time constraints operating during growth. Each growth pattern is described mathematically, which allows for the objective quantification and comparison of the growth patterns by which adult size and function are attained in different parts of the skeleton.

The further objective of this analysis is to evaluate differences in male and female skeletal growth in order to gain a better understanding of the development of secondary sexual dimorphism in modern humans, and provide a basis for future interpretation of its evolutionary and functional significance. The ontogenetic basis of sexual dimorphism in human stature and body weight has been shown to result from a difference in both the rate and duration of growth in males and females and is largely the result of the divergence of male and female growth patterns during adolescence (Willner and Martin, 1985; Harrison et al., 1988). It might be expected that a similar difference in male and female growth trajectories will be found in parts of the skeleton that reflect a general or somatic pattern of growth, but it cannot be assumed that sexual dimorphism will develop in the same way throughout the human skeleton. A detailed analysis of the developmental basis of skeletal dimorphism in different functional regions is necessary to address this problem. The present analysis evaluates the relative contributions of sexual differences in the rate and duration of growth to the development of sexual dimorphism in the post cranial skeleton and compares the age at which sexual differences first occur in different skeletal dimensions.

MATERIALS AND METHODS

Sample

The skeletal remains used for this analysis were excavated from the church crypts of St Bride's Church on Fleet Street, St Barnabas Church and Christ Church, Spitalfields in London, UK (Adams and Reeve, 1987; Bowman et al., 1992; Molleson and Cox, 1993; Scheuer and Bowman, 1995). The individuals used in this study were buried between 1754 and 1851 and are treated as a single population for the present analysis. Each skeleton was found in association with a coffin plate recording the name and often a

title of the individual, and usually the date of death and age at death. In many cases additional documentary evidence was used to give more precise information about the age at death. The documentary sources used for this purpose were baptism records which may include a note of the age of the child in days in the margin, burial registers which usually give the age of the deceased, and death certificates for individuals buried after the introduction of civil registration in 1837. Using the coffin plate and documentary information, the ages at death could usually be determined to the nearest month, giving a maximum error of 2 weeks for the calculated age at death. For many individuals the age of death is known to within a day. The age at death of the adults and a small number of the older juveniles is recorded in years. The sex of each skeleton was inferred from the name and title on the coffin plate.

The measured sample comprises 94 juveniles aged between birth and 20 years and 98 adults aged between 20 and 60 years. Epiphyseal fusion of the long bones and basi-occipital synchondrosis are complete by age 20 in all individuals in this sample, but the stage of eruption of the third molars is variable. Individuals with ages at death of 60 years or older are not included in the analysis in order to avoid the possible effect of age related change associated with tooth loss and bone resorption.

Measurements

Measurements were selected as representative of all regions of the skull and post cranial skeleton. Some of the variables used in this analysis are standard anthropological measurements (Howells, 1973; Bass, 1986), but since many standard measurements cannot be made on infants because the cranial bones are disarticulated, additional measurements are included which can be taken on individuals of all ages. All of the variables analysed for this study can be measured on an isolated bone. This means that the observed changes in each dimension are a true reflection of growth rather than local displacement caused by growth in adjacent regions of the skull (Moore and Lavelle, 1974).

Growth patterns are described for 34 variables measured on the cranium and mandible and 25 variables measured on the post cranial skeleton. Each variable has data for at least 12 juveniles of each sex. The analysis is limited to variables that can be measured from infancy since the absence of measurements from young individuals can distort the shape of the fitted curve. Most of the variables can be measured at birth and at all subsequent ages. Postorbital breadth, maximum frontal breadth and biorbital breadth can be measured following closure of the medio-frontal suture. This occurs between the ages of 8 months and 10 months in non-metopic individuals. Mandibular length can be measured following fusion of the mandibular symphysis, which takes place between 5 and 8 months in the present sample. Fusion of the squamous and condylar parts of the occipital bone occurs at around 1 year and is necessary for most measurements of the occipital and foramen magnum.

Correction for epiphyseal union

Several of the post cranial measurements are affected by epiphyseal fusion. The measurement of maximum iliac breadth is taken excluding the bone added by fusion of the epiphysis at the iliac crest. Fusion of a flake-like epiphysis at the sternal end of the clavicle has a minimal effect on overall length of this bone. The long bone measurements of the adults include epiphyses at both ends, whereas the measurements of most of the juveniles are of the diaphysis only. The measurements of the older children may be taken with both, neither or one of the epiphyses present. No attempt was made to measure diaphysis length with the loose epiphyses held in position because epiphyses are commonly missing and error is introduced by the absence of the cartilage that separates the diaphysis and epiphyses during life.

In order to make the measurements of all of the individuals comparable, the measured long bone length must be reduced by an amount that reflects the size of the epiphyses in cases where fusion has occurred. Once epiphyseal fusion has taken place, radiographs are necessary to determine the size

of the epiphyses. In adolescents and young adults, lines indicating the position of epiphyseal fusion may be visible on a radiograph of a long bone. Radiographs were made of the long bones of a sample of 12 young adults from Spitalfields. The size of the epiphyses is calculated as the difference between the total long bone length and diaphysis length, as measured on the radiograph. Multiple regression analysis was carried out to determine whether the variation in the size of the epiphyses is related to the length of the long bone or the sex of the individual. Sex proved to be a significant source of variation in the size of the epiphyses of the tibia, so separate epiphyseal corrections were calculated for males and females. The size of the epiphyses of the radius is significantly related to the length of the diaphysis. A separate epiphyseal correction for each individual was determined according to the diaphysis length of the radius. The epiphyseal correction for the femur, humerus, ulna and fibula was calculated as the mean size of the epiphyses of all the individuals measured. Half of the appropriate epiphyseal correction was used for individuals in which fusion had only occurred at one end of the long bone.

Curve fitting

Skeletal samples are only suitable for cross-sectional growth studies. In this type of analysis individuals are measured only once and the pattern of growth is inferred from the mean size at successive chronological ages. Most skeletal growth studies use successive mean values calculated from the measurements of a group of individuals showing a particular range of dental or osseous ages (e.g., Johnston, 1962), or a particular stage of dental development (Sundick, 1978). The outcome may be influenced by small or unbalanced sample sizes, particularly in older age ranges, giving a false impression of erratic size changes with age. For the present analysis a curve was fitted to describe the pattern of growth of each variable. Every individual on which a measurement could be made was included in the analysis of each variable so the sample size and age distribution vary. All of the data points, representing size and chronological

age of each individual, were given equal weight in the pattern of growth described. Adult measurements were included so as to avoid assumptions about final size or the age at which growth is complete. These parameters can be determined from the fitted curve. Each growth pattern is described by an equation that allows for the non-subjective comparison of the growth of different variables and of males and females.

Curves were fitted using SPSS Release 6. The curve fitting proceeds in an iterative manner until an optimisation process converges. The values calculated for the curve parameters represent one of the best possible fits of the specified equation to the data. The ages at death were converted from the interval between birth and death to the interval between conception and death, by adding 0.75 to the age at death. This adjustment is preferable for curves that are constrained to go through the origin. The ages that are shown on the graphs and figures have been readjusted to postnatal age.

Visual inspection of the scatter plots of size against age of a sample of variables indicates considerable variation in the underlying growth patterns. The use of a single type of growth curve allows for the direct comparison of the growth of different variables. This curve should be flexible enough to give an accurate description of the growth of every variable, without introducing artefacts that cannot be supported theoretically. Curves such as the polynomial that allow for a decrease in size are unsuitable since growth, by definition, involves an increase in size (Roche, 1986). The growth models used for the present analysis do not incorporate a change in growth rate at adolescence since high velocity growth events that are imperfectly synchronised between individuals, such as the adolescent growth spurt, are disguised in cross sectional growth data (Tanner et al., 1966). One characteristic of every variable is that the distribution of data points is asymptotic. Five asymptotic equations were tested to find an appropriate model.

The most commonly used asymptotic growth curves are the logistic and the Gompertz (Laird, 1965; Zeger and Harlow, 1987; German et al., 1994). These curves are sig-

moid and will tend towards a finite value when extrapolated in either direction. Since the logistic curve is constrained to be symmetrical about the point of inflexion the more flexible Gompertz curve (equation 1) was considered to be more suitable for this analysis. The Gompertz equation can be modified to constrain the lower asymptote to zero by setting parameter c of the equation at zero (equation 2).

$$y = c + a \cdot \exp(-\exp(-b \cdot (x - m))) \quad (1, 2)$$

where $a + c$ = upper asymptote, c = lower asymptote (variable or fixed at zero), m = point of inflexion, b = slope parameter, and x = age.

Equations 1 and 2 are not constrained to go through the origin which is represented by the point of conception, and fail to describe growth prior to the age at which data are available. The fitted curves may lie a considerable distance from the lower asymptote at the point of conception ($x = 0$), giving a false impression of growth before conception. An ideal growth curve for this kind of data would pass through the origin and tend towards an upper asymptote within the range of the data (Jolicoeur, 1985; Lebeau et al., 1986). Three further equations were tested which meet these criteria. Jolicoeur (1985) uses a three parameter curve (equation 3) to describe somatic growth. This curve is derived from the logistic curve by replacing t (time) by its natural logarithm.

$$y = a/(1 + d/x^c) \quad (3)$$

where a = upper asymptote, c = exponent (variable), d = time scale factor, and x = age.

Lebeau et al. (1986) demonstrate the use of a modified version of the von Bertalanffy curve to describe cross-sectional growth. In the first version of this equation (equation 4) the exponent c is fixed at 1 and in the second version (equation 5), c is allowed to vary.

$$y = a[1 - \exp(-x/d)]^c \quad (4, 5)$$

where a = upper asymptote, d = time scale factor, c = exponent (fixed at 1 or variable), and x = age.

Three separate tests were carried out in order to decide which of the five curves is most suitable for the analysis of human skeletal growth data. These tests were made

TABLE 1. *Adjusted R-squared values for the fitted curves*

Variable	Gompertz 1	Gompertz 2	Jolicoeur 3	Lebeau 4	Lebeau 5
Humerus length	0.965	0.965	0.952	0.941	0.960
Minimum ramus breadth	0.704	0.705	0.711	0.594	0.714
Mandibular length	0.908	0.963	0.898	0.787	0.905
Scapula breadth	0.928	0.927	0.919	0.873	0.924
Minimum ulna diameter	0.852	0.853	0.815	0.751	0.857
Maximum frontal breadth	0.468	0.468	0.466	0.451	0.467

on the data for maximum frontal breadth, minimum ramus breadth, maximum mandibular length, humerus length, maximum scapula breadth and minimum ulna diameter. Adjusted R-squared values were calculated for the curves fitted to each variable using each of the five equations described above (Table 1). The adjusted R-squared is less sensitive to the addition of extra terms to the equation, and is a more appropriate measure of goodness of fit than the conventional R-squared which is likely to increase with the addition of extra terms to the model. The adjusted R-squared values do not discriminate particularly well between the equations, although the values for Lebeau's curve (equation 4) are consistently lower than those of the other four equations.

The second test examined the scatter of data points about the fitted curves to determine whether any of the equations results in regular over- or underestimation of size at any stage during growth. The distribution of residuals about the fitted line should be symmetrical at all ages. The upper asymptote should be reached well within the range of the data and should have a value close to mean adult size. On the basis of this test, Jolicoeur's curve (equation 3) and Lebeau's curve (equation 4) were rejected. Jolicoeur's curve (equation 3) frequently fails to come close to the upper asymptote within the range of the data. Lebeau's curve (equation 4) consistently overestimates size between infancy and adolescence. The Gompertz curves (equations 1 and 2) describe the growth of all of the variables fairly well, but tend to overestimate size during infancy. The modified version of Lebeau's curve (equation 5) gives a good estimate of size during infancy, and a reasonably good fit to all of the measurements tested apart from humerus length.

The third test was designed to determine which equation produced the least distortion from the curve fitted to the entire data set when the data for the youngest individuals are excluded. This is important because not all of the cranial variables can be measured at birth. This test was carried out using equations 1, 2 and 5. Each equation was fitted to the entire data set, then to a data set containing individuals aged 1 year and above, and finally to a data set containing individuals aged 2 years and above. Changes to the shape of the fitted curve caused by the removal (or absence) of values for very young children are more predictable and less severe for the modified Gompertz curve (equation 2) than for the other curves.

On the basis of these tests the modified Gompertz curve (equation 2) was selected as the most appropriate model for this analysis of skeletal growth. A standard method was used to fit a curve to each of the variables. First a curve was fitted to the complete data set, including males and females of all ages. The curve fitting process requires that initial values be suggested for each of the unknown parameters in the equation. For each variable the mean adult value was suggested for the upper asymptote (a), and a value of 0.2 for the slope (b) and 0 for the point of inflexion (m). Separate male and female growth patterns were derived for the post cranial variables. All of the post cranial variables can be measured from birth on a minimum of 20 juveniles of each sex. The initial values suggested for each parameter were the final values for the combined male and female curve.

The male and female curves can be used to determine the proportion of sexual dimorphism resulting from differences in growth rate and the proportion resulting from a

difference in the duration of male and female growth (Leigh, 1992). The proportion of sexual dimorphism which can be attributed to sexual differences in growth rate was calculated by dividing the size difference between males and females at the age at which female growth is complete into the difference in the mean size of adult males and females. The proportion of sexual dimorphism that is caused by differences in the duration of male and female growth was calculated as $(1 - \text{proportion caused by rate})$. The required parameters were derived from the equations of the fitted curves. The age at which female growth is complete cannot be determined exactly using an asymptotic curve, so the endpoint of growth was considered to be the age at which 95% of adult size is attained. The size of males at the age at which female growth is complete was determined by feeding this age into the equation for the male growth curve. The difference in adult size was determined as 95% of the difference between the male and female asymptotes.

The male and female growth patterns were used to give an indication of the age at which sexual dimorphism develops in each variable. In all of the skeletal dimensions the range of male and female values overlaps throughout the growth period and in adults. This reflects the relatively low level of sexual dimorphism in modern humans. For this analysis sexual dimorphism was considered to be present from the age at which male size, as determined from the fitted curve, is 1.035 times greater than female size, since sexual differences in the adult sample were found to be significant in variables with this amount or a higher level of sexual dimorphism.

RESULTS

The fitted curves describe the growth patterns of 59 skeletal variables and form the basis for an objective assessment of the relative growth of the different functional regions of the human skeleton. Comparisons are made on the basis of the percentage of adult size attained at successive chronological ages. This allows the growth of different variables to be compared independently of size and is in effect a measure of maturation

rather than growth (Roche, 1992). The percentage of adult size at a given age was calculated by dividing the size of the variable, determined from the equation describing the curve, into estimated adult size. The upper asymptote of the curve, indicated by parameter a in the Gompertz equation, was used as an estimate of adult size.

The range of variation present in the human skeleton is illustrated by the growth patterns of the six variables shown in Figure 1. In terms of their progress towards the attainment of adult size and functional capacity, the cranial and mandibular variables are advanced over the post cranial variables throughout infancy and childhood. At 1 year the greatest contrast is between the frontal bone which has grown to more than 80% of adult breadth and the long bones which are only about 30% of adult length. In general, the skeletal dimensions maintain the same relative positions in terms of percentage of adult size attained for most of the growth period. The long bone lengths differ in this respect, overtaking the other post cranial dimensions during early childhood.

In Figure 2 the variables are plotted according to the ages at which 70% and 90% of adult size are reached. There is a marked contrast between the distribution of cranial and mandibular variables and post cranial variables (Fig. 2). The distinction is most marked in the early growth phase. There is no overlap between the cranial and mandibular variables and post cranial variables in the age range at which 70% of adult size is reached, but considerable overlap in the age range at which 90% of adult size is attained. This is the result of considerable variation in maturation rate among cranial and mandibular variables during the later phase of growth.

The 59 variables are divided into groups according to the ages at which 70% and 90% of adult size are attained. Divisions are made at 6 year intervals on both axes (Fig. 2). The group boundaries (6, 12 and 18 years) roughly correspond to the age of eruption of the three permanent molars. As such they are recognisable developmental landmarks when dealing with skeletal material. Table 2 lists the variables by group together with ages at which 70% and 90% of

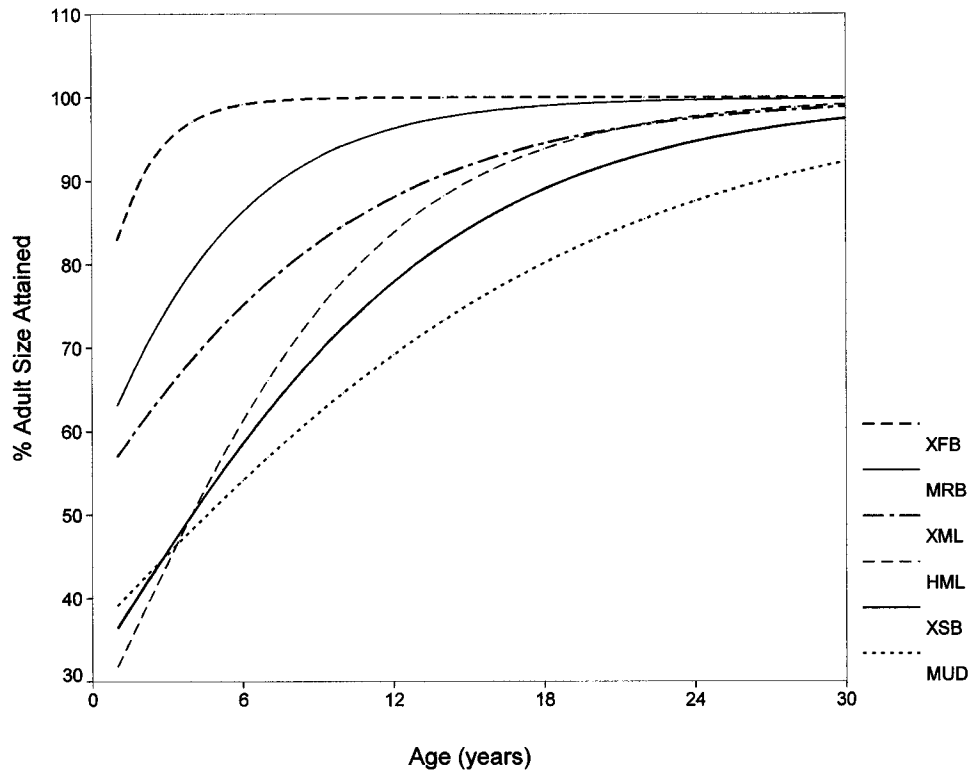


Fig. 1. Percentage of adult size attained against age for six variables measured on the human skeleton, showing the range of variation in growth patterns. XFB = maximum frontal breadth, MRB = minimum ramus breadth, XML = maximum mandibular length, HML = humerus length, XSB = maximum scapula breadth, MUD = minimum ulna diameter.

adult size are reached. The variables in each of the groups follow a characteristic pattern of growth. Early-early growing variables attain 90% of adult size by age 6 years. Early-intermediate growing variables attain 70% of adult size by 6 years and 90% of adult size between ages 6 and 12 years. Early-late growing variables attain 70% of adult size by 6 years and 90% of adult size between ages 12 and 18 years. Intermediate-late growing variables attain 70% of adult size between ages 6 and 12 years and 90% of adult size between 12 and 18 years. Intermediate-very late growing variables attain 70% of adult size between ages 6 and 12 years and 90% of adult size between 18 and 24 years.

A more detailed representation of the growth of the 34 cranial and mandibular variables is shown in Figure 3. The cranial base, brain case and upper facial region

follow an early-early or early-intermediate growth pattern, in which 90% of adult size is attained before age 12 years. The earliest growing variables are measured on the brain case and around the foramen magnum, reflecting a very early neural growth pattern. The variables measured on the malar bone and across the orbits are in the second group of early-intermediate growing variables, together with measurements of the condylar part of the occipital bone. The mandibular variables occur in all five of the groups. The maximum breadth of the mandibular body shows a very early growth pattern. The breadths of the mandible, measured across the condyles, gonion and coronoid processes, group with measurements of the palate and have an early-late pattern of growth. In the early stages of growth, the slowest growing mandibular variables are measurements of length and height, particularly those dimen-

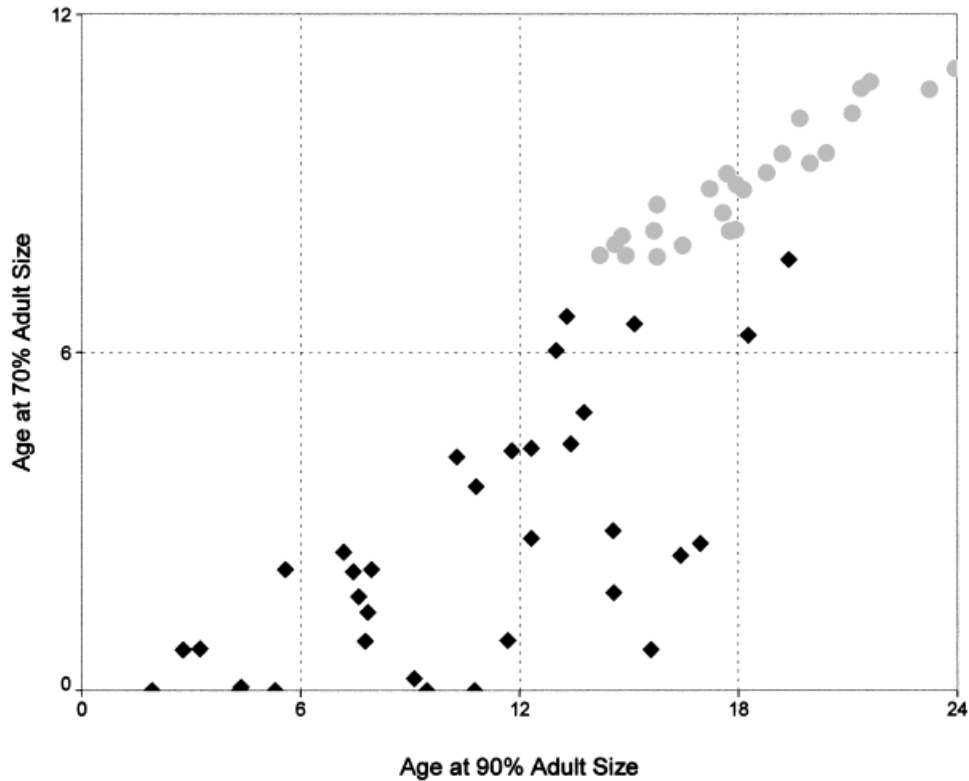


Fig. 2. Age at which 70% of adult size is attained against age at which 90% of adult size is attained in 34 variables measured on the cranium and mandible (diamonds) and 25 variables measured on the post cranial skeleton (circles).

sions which incorporate the mandibular condyle. These variables catch up with the palate and mandible breadths during the later period of growth and attain 90% of adult size at a similar age. The slowest growing cranial variables are the height and breadth of the mastoid process.

The growth patterns of the 25 post cranial variables are represented in Figure 4. The earliest post cranial variables to attain adult size are the six long bone lengths, which are tightly grouped together in the intermediate-late growth group. The growth of the clavicle, pelvis and scapula is completed slightly later than that of the long bone lengths. The slowest growing variables are the diameters of the long bones and clavicle. The growth of many of these dimensions continues into early adulthood.

The mean levels of sexual dimorphism of the variables in the five growth groups are

given in Table 3. There is an increasing trend in the mean level of sexual dimorphism across the five groups suggesting a relationship between the development of sexual dimorphism and the pattern of growth. The differences between successive group means were tested for significance using the Mann-Whitney test. Significant differences in mean sexual dimorphism occur between the early-late and intermediate-late (two-tailed, $P < 0.01$) and the intermediate-late and intermediate-very late growth groups (two-tailed, $P < 0.05$). Linear regression analysis was carried out to examine the relationship between the age at 90% of adult size and sexual dimorphism. There is a highly significant positive relationship between the two variables ($P < 0.001$, $r^2 = 0.496$). The result suggests that about half of the variation in sexual dimorphism is

TABLE 2. Growth groups based on the ages of attainment of 70% and 90% adult size, together with the parameter values for the fitted Gompertz equations¹

	a	b	m	70%	90%
Early-early growth					
Maximum frontal breadth	116.91	0.62	-1.70	by birth	1.9
Maximum occipital condyle breadth	10.84	0.59	-1.02	0.7	2.8
Maximum mandibular corpus breadth	14.60	0.49	-1.37	0.7	3.2
Postorbital breadth	93.96	0.27	-3.88	by birth	4.3
Posterior inter-occipital condylar distance	42.31	0.28	-4.32	0.1	4.4
Foramen magnum breadth	29.66	0.15	-10.07	by birth	5.3
Anterior inter-occipital condylar distance	20.17	0.35	-0.76	2.1	5.6
Early-intermediate growth					
Maximum malar length	50.04	0.26	-2.20	2.5	7.2
Minimum ramus breadth	29.01	0.23	-2.39	2.1	7.4
Distance across jugular processes	71.37	0.21	-4.08	1.7	7.6
Maximum external palate breadth	57.89	0.19	-4.07	1.4	7.8
Orbital width	38.10	0.18	-4.94	0.9	7.8
Malar height	21.16	0.18	-4.43	2.2	7.9
Distance between mental foramina	43.63	0.14	-7.31	0.2	9.1
Minimum occipital breadth	76.77	0.12	-10.34	by birth	9.5
Mandibular notch depth	12.29	0.20	-1.03	4.1	10.3
Bifrontal breadth	94.66	0.11	-9.32	by birth	10.8
Inferior malar length	32.72	0.17	-3.08	3.6	10.8
Bicoronoid distance	93.57	0.11	-8.23	0.9	11.7
Mandibular corpus length	83.35	0.16	-2.10	4.3	11.8
Early-late growth					
Coronoid-condyle distance	25.67	0.15	-2.49	4.3	12.3
Maximum internal palate breadth	34.82	0.13	-5.49	2.7	12.4
Maximum mandibular length	102.02	0.13	-3.26	4.4	13.4
Anterior mandibular height	31.78	0.14	-2.53	4.9	13.8
Maximum nasal breadth	22.75	0.09	-9.11	1.7	14.6
Bigonial distance	93.63	0.10	-7.07	2.8	14.6
External palate length	43.11	0.08	-11.84	0.7	15.6
Bicondylar distance	113.57	0.09	-9.45	2.4	16.4
Internal palate length	35.49	0.08	-9.52	2.6	17.0
Intermediate-late growth					
Condylar height	57.33	0.18	0.14	6.0	13.0
Anterior mastoid height	17.80	0.18	1.00	6.6	13.3
Fibula length	300.36	0.19	2.24	7.7	14.2
Tibia length	312.00	0.18	2.25	7.9	14.6
Femur length	389.00	0.18	2.37	8.1	14.8
Radius length	202.32	0.17	1.67	7.7	14.9
Coronoid height	60.76	0.14	-0.80	6.5	15.2
Ulna length	226.29	0.16	1.80	8.2	15.7
Minimum tibia diameter	20.96	0.15	0.87	7.7	15.8
Humerus length	227.33	0.17	1.81	8.6	15.8
Clavicle length	139.74	0.14	0.64	7.9	16.5
Maximum iliac breadth	147.52	0.15	1.90	8.9	17.2
Maximum radius diameter	14.88	0.13	0.79	8.5	17.6
Maximum femur diameter	27.27	0.14	1.96	9.2	17.7
Maximum clavicle diameter	11.87	0.13	0.04	8.2	17.8
Minimum radius diameter	11.09	0.12	-0.08	8.2	17.9
Minimum iliac breadth	61.89	0.14	1.40	9.0	17.9
Intermediate-very late growth					
Glenoid cavity breadth	25.34	0.13	1.08	8.9	18.1
Mandibular condyle breadth	19.34	0.10	-3.80	6.3	18.3
Maximum scapula breadth	89.99	0.13	1.07	9.2	18.8
Maximum fibula diameter	14.43	0.13	1.35	9.5	19.2
Mastoid breadth	26.21	0.10	-2.26	7.7	19.4
Maximum tibia diameter	28.72	0.13	2.11	10.2	19.7
Minimum humerus diameter	19.77	0.12	0.40	9.4	20.0
Maximum humerus diameter	20.23	0.11	0.33	9.5	20.4
Maximum ulna diameter	16.38	0.11	1.04	10.2	21.1
Minimum femur diameter	26.38	0.11	1.64	10.7	21.4
Minimum fibula diameter	11.74	0.11	1.68	10.8	21.6
Minimum clavicle diameter	9.44	0.10	0.05	10.7	23.3
Minimum ulna diameter	12.20	0.09	0.13	11.0	24.0

¹ Measurements are in mm.

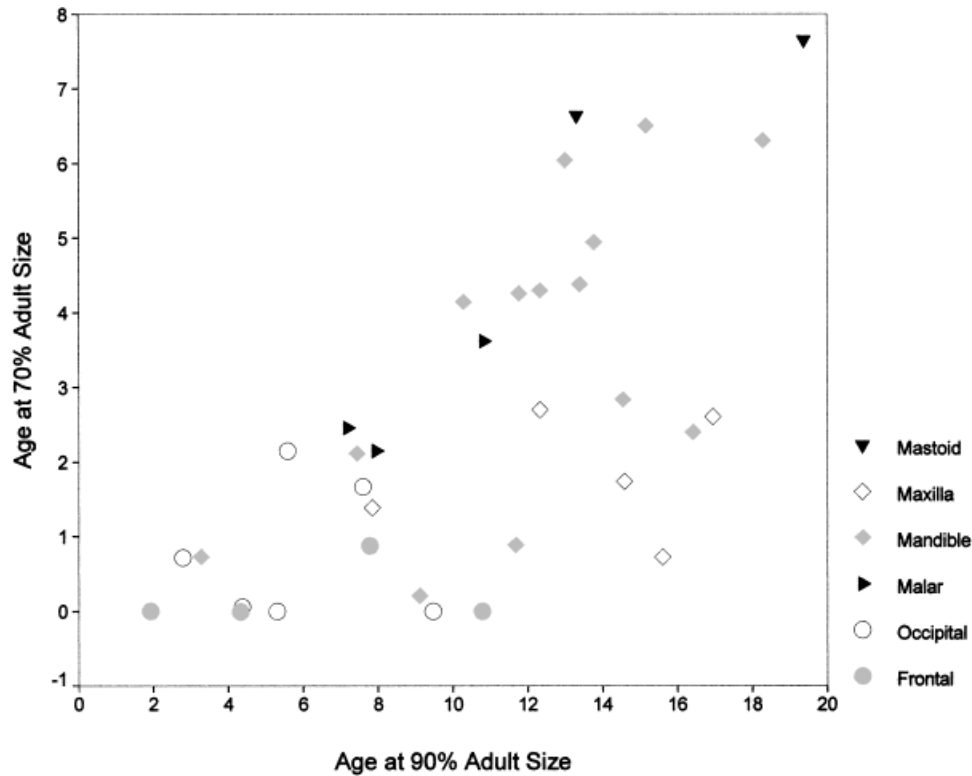


Fig. 3. Age at which 70% of adult size is attained against age at which 90% of adult size is attained in 34 variables measured on the cranium and mandible.

related to the age of attainment of 90% of adult size.

The developmental basis of sexual dimorphism varies within the post cranial skeleton. Sexual dimorphism is caused either by sex differences in growth rate or a combination of sex differences in growth rate and duration. Table 4 shows the proportion of adult sexual dimorphism caused by growth rate differences in each of the post cranial variables and the age at which sexual dimorphism becomes apparent. The variables are ordered according to the proportion of sexual dimorphism resulting from sexually differentiated growth rates. Figure 5 illustrates three different examples of divergent male and female growth patterns.

The analysis reveals a clear difference between the diameters and lengths of the long bones in the developmental basis of sexual dimorphism. Sexual differences in growth rate account for only 19–53%

($x = 34\%$) of sexual dimorphism in long bone length, but for over 60% (61–100%, $x = 80\%$) of sexual dimorphism in the long bone diameters. This difference is reflected in the ages at which sexual differences in size develop. Sexual dimorphism in long bone length develops at adolescence ($x = 15.8$ years) while sexual dimorphism in the long bone diameters develops between birth and adolescence ($x = 2.1$ years). The maximum breadth of the scapula follows an intermediate pattern. Sexual dimorphism in the clavicle, pelvis, and glenoid cavity of the scapula develops prior to adolescence, and is caused mainly by a difference in male and female growth rates. This pattern is more similar to that of the long bone diameters. The maximum breadth of the iliac bone does not show significant sexual dimorphism. Sexual differences in the clavicle dimensions, including length, are already present at birth, suggesting that

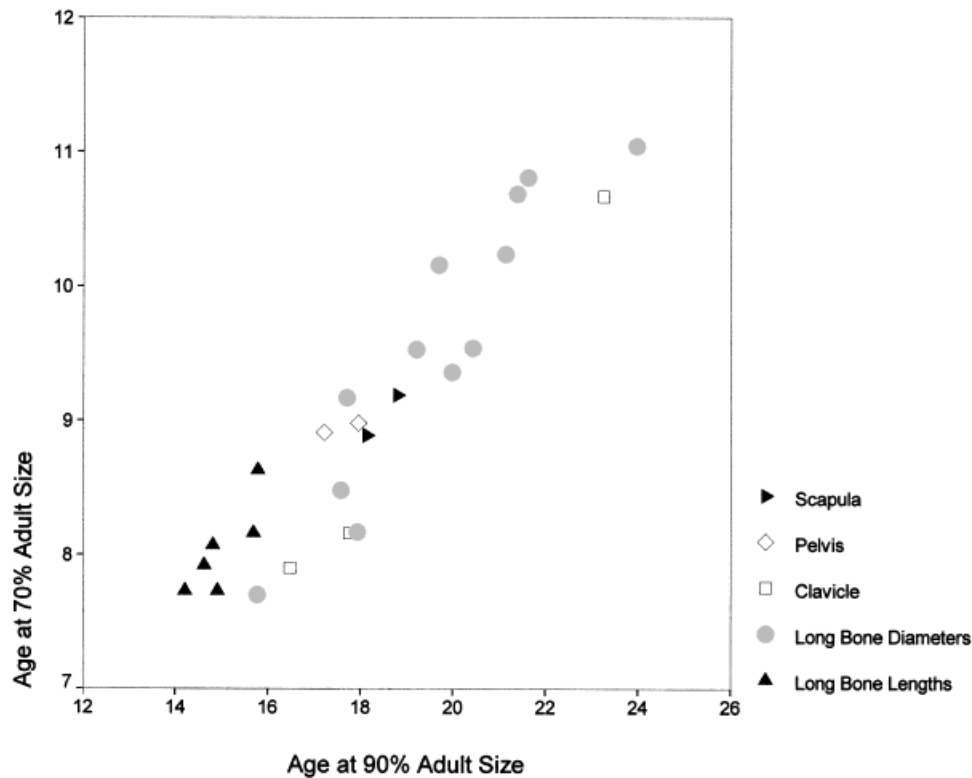


Fig. 4. Age at which 70% of adult size is attained against age at which 90% of adult size is attained in 25 variables measured on the post cranial skeleton.

TABLE 3. Mean sexual dimorphism in the five growth groups

Growth pattern	Number	Mean	S.D.	Range
1. Early	7	104.2	2.1	101.5–107.5
2. Early-intermediate	13	106.3	2.7	101.5–112.3
3. Early-late	9	105.9	3.1	100.6–111.6
4. Intermediate-late	17	111.2	4.1	102.6–119.8
5. Intermediate-very late	13	114.2	3.6	108.9–119.9

this pattern may be typical of variables that measure upper limb robusticity.

DISCUSSION

The curve fitting method used in this analysis allows objective comparisons of the growth of different parts of the skeleton. The fitted curves are not intended to provide exact descriptive models of the growth of each skeletal variable but are used as a

TABLE 4. Proportion of sexual dimorphism resulting from sexual differences in growth rate and the age at which sexual dimorphism develops

Post cranial variable	Rate	Age
Fibula length	0.19	16.1
Femur length	0.28	17.6
Tibia length	0.30	17.3
Humerus length	0.31	16.6
Radius length	0.44	14.3
Ulna length	0.53	13.0
Maximum scapula breadth	0.56	13.7
Maximum clavicle diameter	0.60	0.0
Minimum fibula diameter	0.61	11.2
Maximum femur diameter	0.66	0.0
Maximum radius diameter	0.67	0.0
Minimum tibia diameter	0.72	5.3
Maximum ulna diameter	0.73	0.0
Minimum iliac breadth	0.73	8.6
Minimum clavicle diameter	0.74	0.0
Glenoid cavity breadth	0.78	4.2
Maximum tibia diameter	0.78	4.2
Minimum radius diameter	0.79	0.0
Minimum ulna diameter	0.86	0.0
Maximum humerus diameter	0.90	0.0
Minimum femur diameter	0.93	0.0
Clavicle length	0.95	4.9
Minimum humerus diameter	0.99	1.1
Maximum fibula diameter	1.00	2.3

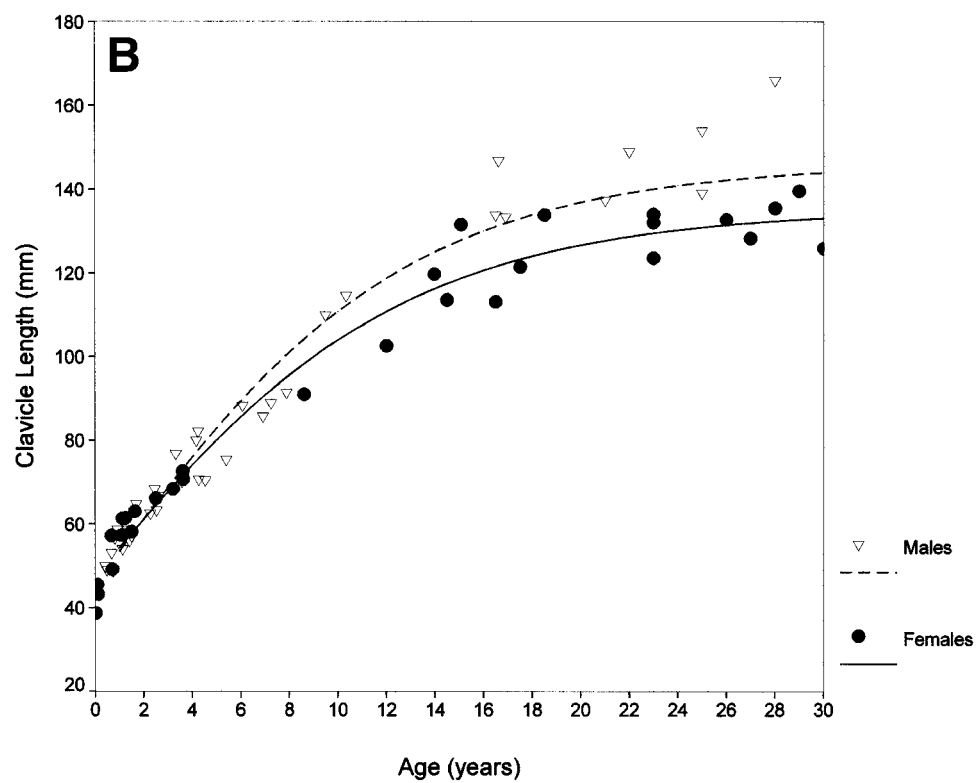
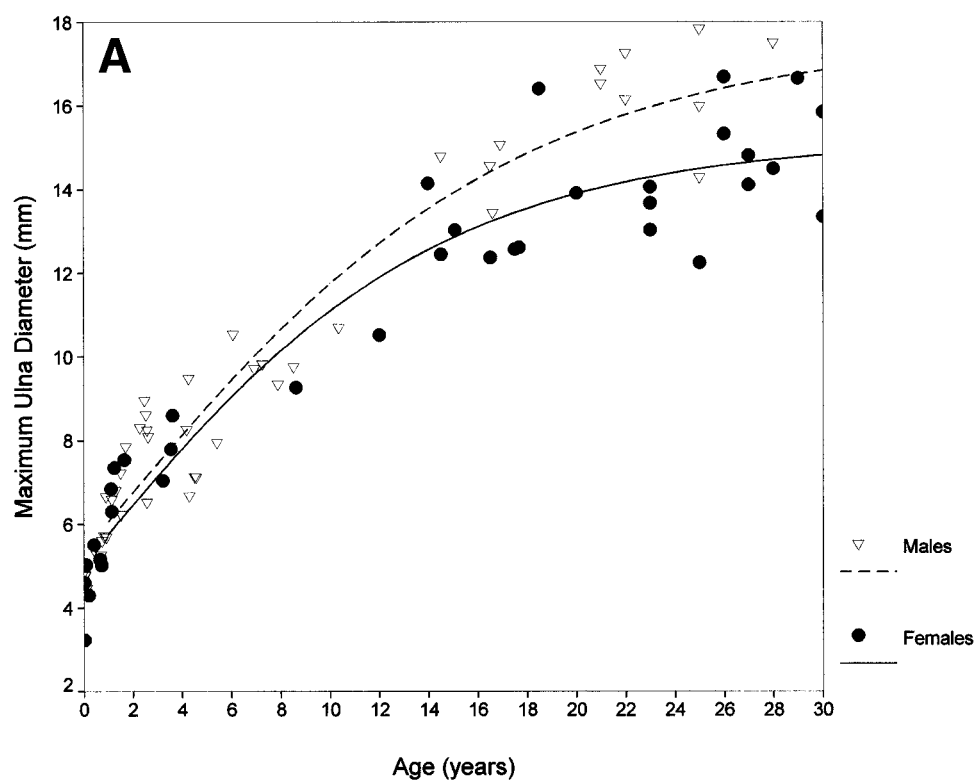


Fig. 5.

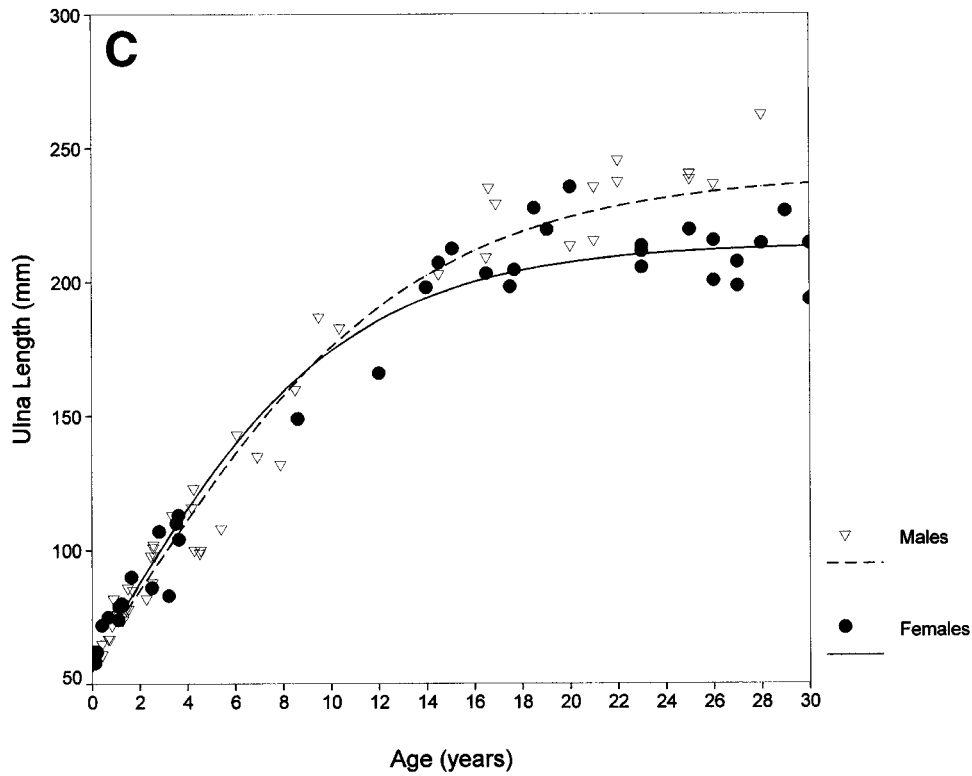


Fig. 5. A-C: Bivariate plots of male and female size against age and the Gompertz curves describing male and female growth. The proportion of sexual dimorphism resulting from sexual differences in growth rate and the age at which sexual dimorphism develops in each variable are given in Table 4.

basis for assessing the diversity of growth patterns in different functional regions of the modern human skeleton. Variation in skeletal growth is considered in terms of the age at which 70% and 90% of adult size are attained. The analysis demonstrates a range of growth patterns from the earliest growing parts of the cranium to the slowest growing long bone diameters. Within this continuum there are consistent spatial and functional patterns across the skeleton reflecting the variable growth patterns of the associated soft tissues and functioning spaces. This is illustrated in the skull by the gradual transition between the early growing neurocranium and the later growing mandibular and mastoid dimensions.

The earliest growing variables are measured on the frontal and occipital bones. The early development of these skeletal regions reflects the growth of the associated neural structures, primarily the brain, eyes and spinal cord. The earliest growing skeletal

dimension is maximum frontal breadth which most closely reflects the growth of the brain. Orbital breadth and bifrontal breadth achieve adult size slightly later and are affected by the adjacent nasal and zygomatic regions as well as the developing orbital mass. The growth of the skeletal structures immediately surrounding the foramen magnum is complete at about 6 years and this parallels the process of occipital fusion. By the age of 6 years the four parts of the occipital are joined and the foramen magnum is fully enclosed by bone.

The growth of the maxillae and mandible is influenced by the development of the dentition as well as the functional requirements of respiration, chewing, swallowing and speech (Goose and Appleton, 1982). The results of the present study demonstrate that the palate and mandible are characterised by fairly rapid early growth and a more variable rate of attainment of adult size. The slowest growing mandibular dimensions re-

flect the height of the mandibular ramus and the size of the mandibular condyle. The growth patterns of the mid-facial region and parts of the cranial base are intermediate between the early growing neural structures and the later growing masticatory apparatus. The growth of these variables is influenced by both functional regions and by the development of the respiratory system.

These results are consistent with previous work on functional cranial analysis. Moss and Young (1960) divided the skull into the neural, orbital and facial regions. The neural region of the skull responds primarily to the growth of the brain (Moss and Young, 1960). The orbital region grows in response to the developing orbital mass while the growth of the mid-facial region is additionally influenced by the developing nasal and oral spaces (Moss, 1973). The extent to which the functional components can be regarded as potentially independent in development and evolution is debated (Moss and Young, 1960; Dullemeijer and Barel, 1977) but it is accepted that parts of the skeleton that form the same skeletal unit must exhibit strongly interdependent growth patterns. In the present study this interdependence is reflected by the relative similarity in growth patterns of variables relating to the same bone or function.

The skeletal growth patterns outlined by this study demonstrate a clear sequence in the development of adult size and function of different skeletal regions. This sequence must be adapted to the energetic constraints imposed by the need to produce and maintain different tissues, and must in addition meet the functional demands of the child at successive stages of development. The earliest growing skeletal elements support and surround the neural structures, indicating that the initial functional requirement of the growing child is to establish the basis for full neurological capacities. The early growth of the brain relative to other functional systems allows time for the development of learned behaviour. The prolonged period between the cessation of brain growth and the onset of puberty appears to be a unique feature of human growth (Watts, 1986; Leigh, 1996) and may be related to the development of human culture and language. The growth of the masticatory system is expected to reflect changes in the nutritional

demands of the body and the way in which these are acquired. The rapid early growth of the palate and mandibular body satisfies the immediate requirement of suckling and is necessary to accommodate the deciduous dentition and the developing crowns of the permanent teeth in the first few years of life.

Growth of the post cranial skeleton is delayed relative to that of the cranium and mandible. This difference is particularly marked in the early period of growth (Figs. 1, 2). Growth of the long bone lengths is complete earlier than the rest of the post cranial skeleton despite the fact that these variables have attained a lower percentage of adult size at birth. The pelvis, scapula and clavicle length complete their growth earlier than the diameters of the long bones and clavicle. The increase in skeletal robusticity, measured here by the growth of the diameters of the long bones and clavicle, continues into adult life and is not constrained by epiphyseal fusion. These results indicate that the full development of locomotory and reproductive functions occurs subsequent to the development of neural and food processing functions. Investment into the strength and durability of the post cranial skeleton through increased robusticity is the final stage of human growth.

The level of sexual dimorphism in different parts of the modern human skeleton varies between dimensions in which there is virtually no sexual dimorphism to dimensions in which males are 20% larger than females. There is a significant relationship between the pattern of growth and the development of sexual dimorphism in the human skeleton. Early growing parts of the skeleton are generally less sexually dimorphic than later growing elements, as suggested by Schultz (1962). There are two possible reasons for this relationship. Males and females might be expected to show similar growth trajectories until adolescence since their functional requirements are more similar prior to sexual maturation (Willner and Martin, 1985). If sexual dimorphism is the result of a late divergence of male and female growth, for example at adolescence, variables in which growth is complete prior to this divergence would not be expected to show sexual dimorphism. Alternatively, if sexual dimorphism is caused by a difference in male and female growth rates, the devel-

opment of sexual dimorphism may be constrained by the time available for sexual differences to accumulate. The evidence from this analysis suggests that both factors are present. There is a trend for increase in sexual dimorphism across all five groups of variables (Table 3) but the only significant increases are between the early-late and intermediate-late and the intermediate-late and intermediate-very late growth groups. Growth of the variables in these three groups is completed during or subsequent to adolescence. However, significant levels of sexual dimorphism also occur in variables that complete their growth prior to adolescence. This outcome reflects the diverse ontogenetic origins of sexual dimorphism within the human skeleton.

A more complete understanding of the development of sexual dimorphism in the human skeleton can be gained from the separate male and female growth patterns. Analysis of the sex specific growth patterns demonstrates that there is considerable diversity in the developmental basis of post cranial sexual dimorphism (Table 4). This is evident both in the proportion of sexual dimorphism resulting from sex differences in growth rate and the age at which sexual dimorphism develops. The development of sexual dimorphism in the human skeleton is clearly not dependent on the presence and timing of growth changes at adolescence. Sexual dimorphism occurs in many parts of the skeleton which complete their growth prior to adolescence and analysis of separate male and female patterns of post cranial growth demonstrates that in most post cranial dimensions, male and female growth trajectories diverge prior to adolescence.

The development of sexual dimorphism in the long bone lengths differs from the more general pattern observed in the post cranial skeleton in two ways. First, males and females follow very similar growth trajectories prior to adolescence, and second the proportion of sexual dimorphism resulting from differences in the duration of male and female growth is higher than in the other post cranial dimensions. The development of sexual dimorphism in the long bone lengths follows the same pattern that has been described for human body weight and stature, with more than half of adult sexual dimorphism resulting from sexual bimatur-

ism (Willner and Martin, 1985; Harrison et al., 1988). The difference in the duration of growth in body weight and height in modern males and females is the result of a difference in the timing of the adolescent growth spurt, which occurs on average about 2 years earlier in females than in males. Since this analysis uses cross sectional growth data no attempt was made to demonstrate the presence or absence of an adolescent growth spurt in any of the skeletal dimensions. The importance of bimaturism in the development of sexual dimorphism in human long bone lengths is reflected by the difference in the average timing of skeletal maturation in males and females. The growth of the long bone lengths ceases with epiphyseal fusion, which on average occurs earlier in females than males (Roche, 1986).

Two factors of fundamental importance to the development of sexual dimorphism are time constraints (acting on the duration of growth) and energetic constraints (acting on the rate of growth) and these may differ between functional regions of the skeleton. Sexual dimorphism can only be acquired through more rapid male growth if nutritional resources are adequate to sustain this without incurring unnecessary metabolic risks. Sexual bimorphism may have evolved in order to increase the time available for growth in the larger males and reduce the risk incurred by rapid growth rates. An alternative theory is that sexual bimaturism, and by extension sexual dimorphism in affected structures, has evolved as an outcome of selective factors differentially affecting male and female life history strategies (Willner and Martin, 1985). The diversity of patterns through which sexual dimorphism develops in different parts of the skeleton and the relationship between the expression of sexual dimorphism in adults and the duration of growth are caused by a complex pattern of interacting factors. These include selection on male and female size, time and energetic factors operating during and after growth and the functional requirements of the growing child at each stage of development.

CONCLUSIONS

A single phase Gompertz equation was used to compare the growth of skeletal dimensions measured across the human skeleton. This method allows variables to be

grouped according to their rate of attainment of adult size. Within the human skeleton there is a range of growth patterns from the earliest growing neural dimensions to the slowest growing long bone diameters. This developmental sequence reflects the early growth of the neural structures relative to the more gradual development of the masticatory structures and the prolonged development of the post cranial skeleton and associated locomotory and reproductive functions. It has yet to be demonstrated to what extent the developmental pattern outlined in this paper is peculiar to modern humans.

This study shows that the development of skeletal sexual dimorphism in a species cannot be considered to be a uniform phenomenon. In humans there are clear differences within the post cranial skeleton in terms of the relative contributions of sexual differences in growth rate and duration to adult sexual dimorphism. The development of sexual dimorphism has to be regarded as the result of a complex pattern of interacting factors.

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